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First discovery of Neogene proboscidean fossils in southeast China

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Abstract *Stegolophodon* is an age-informative genus of mammals that had a widespread distribution during the Neogene. This paper reports the discovery of *Stegolophodon* fossils from the Middle Miocene lower Fotan Formation at the Zhangpu locality, Fujian Province, China. This discovery represents the first evidence of Neogene proboscidean fossils in southeastern China. The newly found molar materials have low tooth crowns, very straight lophs/lophids, and an indistinct median sulcus. The mesoconelets and posterior cingulum are well-developed, while the second posterior pretrite central conule is significantly reduced. These specimens closely resemble *Stegolophodon pseudolatidens* in cheek tooth morphology, and can thus be attributed to the same species. This discovery fills a gap in the fossil record of large mammals in this region during the Neogene and provides valuable insights into the evolution of proboscideans and paleoenvironments.

Key words southeastern China, Middle Miocene, proboscidean, *Stegolophodon*, morphology

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1 Introduction

The Miocene epoch (23–5.3 Ma) is a significant geological period in Earth's history, characterized by notable global climate changes and the rapid evolution of mammals. Proboscideans, in particular, thrived during the Early to Middle Miocene in Eurasia, exhibiting

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a wide distribution and diverse species across northern and western China. However, there have been no records of proboscidean fossils from the southeastern coastal regions of China, largely due to the rarity of Tertiary sediments in this area.

During an investigation of the amber fossil site in Zhangpu, Fujian, the Fujian Institute of Geological Survey unexpectedly discovered fossils of *Stegolophodon*, a proboscidean from the Middle Miocene period. *Stegolophodon* had a wide distribution across Asia from the Early Miocene to the Late Miocene, with fossil records found in China, Japan, Thailand, Myanmar, India, and Pakistan (Saegusa, 2005; Iizumi et al., 2021). This genus is characterized by its tetralophodont, brachyodont intermediate molars, upper tusks with longitudinal enamel bands, and elongated mandibular symphysis with a pair of lower tusks. The upper molar M3 typically has 5 to 6 lophs and the lower molar m3 has 5 to 8 lophids, with the number of lophs/lophids gradually increasing with evolutionary progression (Li et al., 2020).

Currently, more than seven species of *Stegolophodon* are recognized (Saegusa et al., 2005; Li et al., 2020), including *Sl. hueiheensis*, *Sl. nasaiensis*, *Sl. praelatidens*, *Sl. latidens*, *Sl. cautleyi*, *Sl. stegodontoides*, and *Sl. pseudolatidens* (Li et al., 2020). The type species, *Sl. latidens*, was described from the Irrawaddy Formation of Myanmar. According to Kalb and Mebrate (1993), and Kalb et al. (1996), *Stegolophodon* and *Stegodon* are placed at the base of the Elephantidae family, though these genera do not form a monophyletic group. However, continuous fossil records from East, Southeast, and South Asia provide morphological transitions between the two genera. The evolution of *Stegolophodon* and its closely related groups laid the foundation for the emergence of *Stegodon*.

Limited *Stegolophodon* material has been recovered and reported from China, with fossils of *Sl. hueiheensis* from Jiangsu (Chow, 1959), *Sl. latidens* and *Sl. stegodontoides* from Yunan (Wang et al., 2015; Li et al., 2020). These findings clearly indicate that *Stegolophodon* had reached China. However, until now, *Stegolophodon* has never been reported from southeastern China, and the paleoecological significance of *Stegolophodon* in China has remained poorly understood.

In this study, we report the recently discovered molar materials of *Stegolophodon pseudolatidens* from the Fotan Formation at the Zhangpu locality in southeastern China (Fig. 1). Based on measurements and comparisons of the molar morphology with other species of *Stegolophodon*, we determine that the new materials closely resemble *Sl. pseudolatidens* and can be assigned to the same species. The discovery is of significant importance for understanding of the evolution and distribution of *Stegolophodon* across Asia.

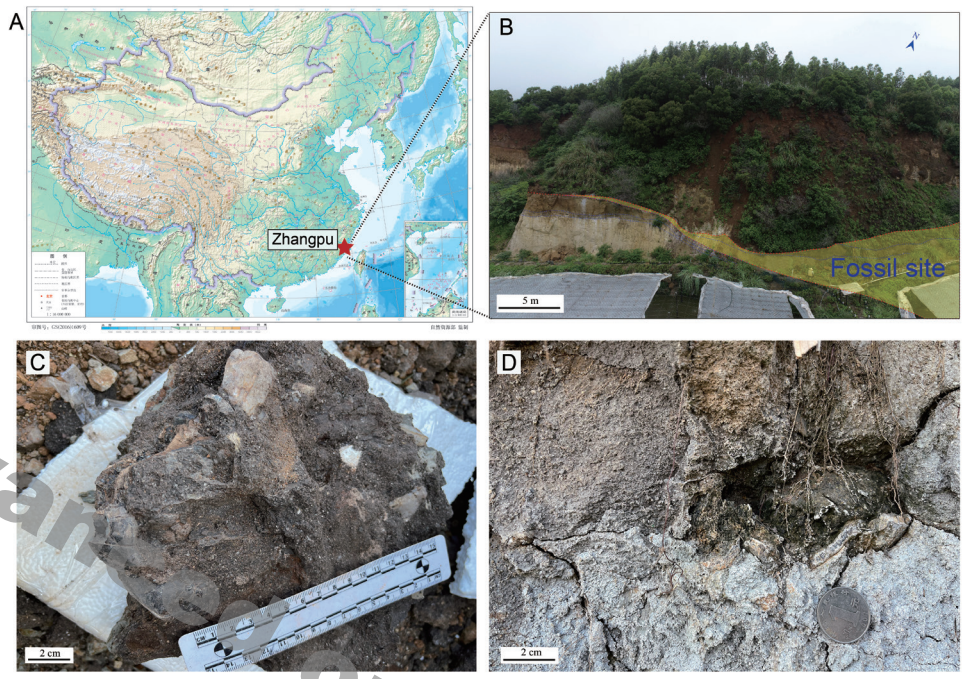

Fig. 1 Geographic location of the *Stegolophodon pseudolatidens* fossils from Zhangpu, Fujian Province, China
A. geomorphology of East Asia; the red star denotes the location of the study areas Map Review (Inspection) Number: GS(2016)1609; B. photograph of the outcrop at the new fossil locality; with the yellow region highlighting the amber-bearing layers; C. deposition of specimen IVPP V33469; D. deposition of specimen FJZP001

2 Materials and methods

The new materials include four incomplete upper and lower molars, as well as a small tip of right upper tusk. The molar measurement protocol and dental terminology follow Tassy (2014), Wang et al. (2017) and Li et al. (2019) which is presented in Fig. 2. Measurements were taken with digital calipers (in mm). All the materials described in this paper are housed in the IVPP and FIGS.

Abbreviations FIGS, Fujian Institute of Geological Survey, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; H, maximal height; Hpo, maximal height of the posttrite side; Hpr, maximal height of the pretrite side; I, index; L, length; l, left; M, upper molar; m, lower molar; r, right; W, maximal width; W1, W2, and W3, width at the first, second, and third loph(id)s.

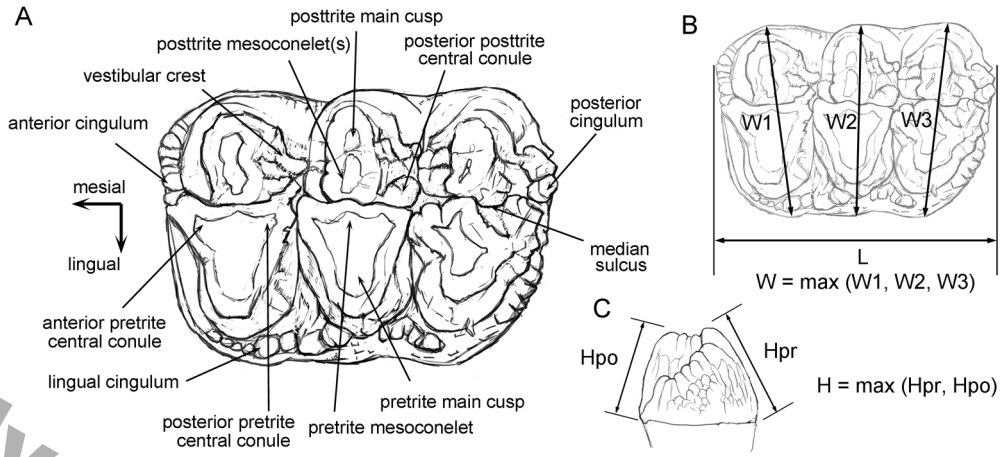

Fig. 2 Tooth terminology and measurements (after Tassy, 2014; Wang et al., 2017; Li et al., 2019)
A. occlusal terminology of a gomphotheriid tooth; B. length and width measurements of a left M2, occlusal view; C. height measurements on a molar, distal view

3 Geographic and geological settings

The Zhangpu Basin in Fujian Provence is located along the southeastern coast of China, within the Mesozoic magmatic belt and the Pingtan-Dongshan shear zone (Tang, 2022) (Fig. 1A). The Zhangpu Basin is one of the most significant Miocene fossil-rich regions of coastal China, known for its abundant amber and diverse plant fossils. This region has been extensively studied by many paleontologists and geologists across China. Reported plant macrofossils include 72 species from 40 genera and 25 families, with angiosperms being the predominant group (Wang et al., 2019). The Zhangpu amber contains a large variety of plant and animal fossils, including arthropods from over 250 families across 22 orders, making it the largest amber biota in China and the third largest in the world (Wang et al., 2021).

The new mammal fossils in this study were excavated from the Middle Miocene Fotan Formation. The mammal-bearing layer is located within the layer of amber sedimentary deposits (Fig. 1B). We investigated the fossil site section, and a summarized stratigraphic column is presented in Fig. 3. Based on the stratigraphic correlation, the 3–5 sedimentary sandy mudstone layers are characterized by the presence of amber. The new *Stegolophodon* material was found in the fourth pebbly sandy mudstone layer. K-Ar age determination of the basalt in the fossil-bearing strata places the age of the lower Fotan Formation at approximately 15.5 Ma, confirming its Middle Miocene age.

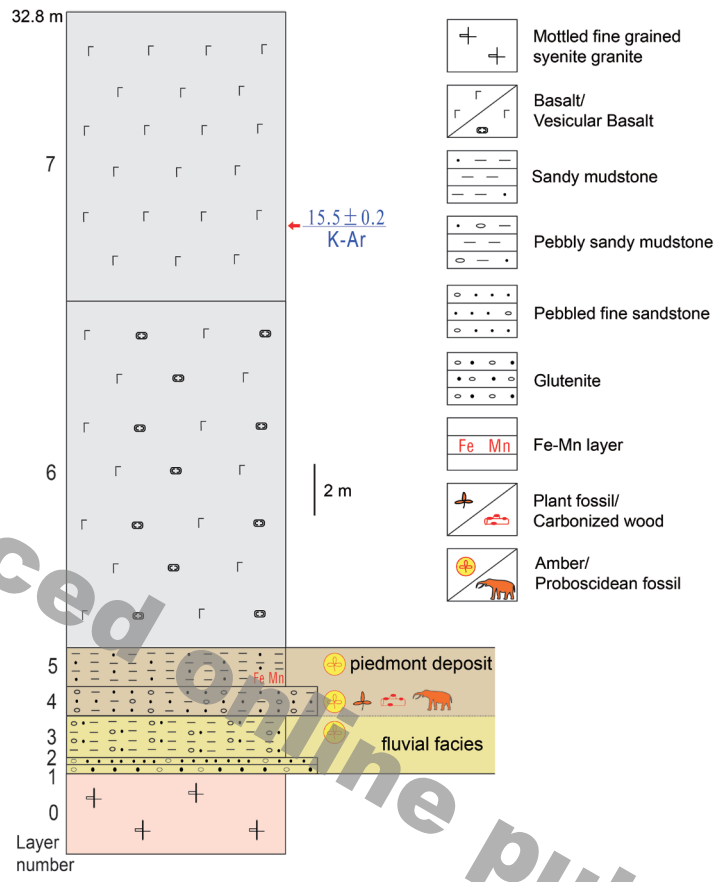

Fig. 3 Stratigraphic column showing the five layers of the Futan Formation at the Zhangpu locality
The new *Stegolophodon* remains were found in the fourth pebbly sandy mudstone layer

4 Systematic palaeontology

Order Proboscidea Illiger, 1811

Family Stegodontidae Osborn, 1918

Genus *Stegolophodon* Schlesinger, 1917

Type species *Stegolophodon latidens* (Clift, 1828).

Type locality Irrawaddy River, Myanmar; early Late Miocene.

***Stegolophodon pseudolatidens* (Yabe, 1950)**

Age and occurrence The late Early Miocene, ~18–16 Ma, Japan.

Material in the present article IVPP V33469: an incomplete left M2, from Zhangpu Fujian, China, is housed at IVPP. FJZP001: an incomplete left M3; FJZP002: an incomplete right lower m2; FJZP003: an incomplete M3; FJZP004: a right upper tusk tip. All from Zhangpu Fujian, China, and are housed at FIGS.

Age and horizon Fotan Formation, Fujian Province; Middle Miocene, ~15.5 Ma.

Description FJZP001 (Fig. 4A–C) is an incomplete left M3, moderately worn, with only the last 3.5 lophs preserved. The tooth crown is relatively low and the interlophs are relatively wide mesiodistally. The median sulcus is not prominent. The lophs are very straight and almost perpendicular to the long axis of the molar. The preserved first loph (which is speculated to be the second loph) is heavily broken and deeply worn; the posterior pretrite central conule is identifiable, while the posterior posttrite central conule is absent. However, there is no posterior pretrite central conule on the remaining lophs. The third and fourth lophs contain two main cusps each and several divided mesoconelets. The mesoconelets are well-developed and are nearly the same size as the main cusps. The posterior cingulum is well-developed forms the last loph, consisting of multiple closely arranged conelets.

FJZP004 (Fig. 4D–G) is the very distal section of a small upper tusk. It measures approximately 7 cm in length and 2 cm in width. The tip is very straight and tapers anteriorly, with no wear facet. An enamel band is present on one side. The shape of the cross-section is irregular triangle in the middle segment.

FJZP002 (Fig. 4H–J) is an incomplete right lower m2, with only the front 2.5 lophids preserved. The crown is relatively low and the interlophids are relatively narrow. The first lophid is moderately worn, and the anterior pretrite central conule is connected to the mesial cingulum. A big posterior pretrite central conule is present. The mesoconelet is well-developed, and the wear pattern on both sides of the pretrite half-loph and posttrite half-loph forms a gourd shape. The second and third lophids are deeply worn, and none of the important morphological features are recognizable.

FJZP003 (Fig. 4K–M) is an incomplete M3. The lophids are straight, but no other morphological details are clear, as the speciemen is heavily worn and poorly preserved.

IVPP V33469 (Fig. 4N–P) is an incomplete left M2. The first loph is deeply worn, and the anterior pretrite central conule is connected to the mesial cingulum. Both the posterior pretrite and posttrite central conules are absent. The second loph is broken, with only the posttrite cusp remaining.

Table 1 Tooth measurements of new *Stegolophodon pseudolatidens* materials from southeastern China (mm)

Specimen	Locus	L	Wmax	W1	W2	W3	W4	W5	Hpo	I=W/L
FJZP001	l M3	146.43+	103.06	—	78.26+	103.06	94.56	81.42	41.23	0.70
FJZP002	r m2	101.98+	75.26	70.03	75.26	—	—	—	38.81+	0.74
FJZP003	M/m3	—	97.91+	—	97.91+	71.80+	—	—	41.47+	—
IVPP V33469	r M2	95.45+	88.07	88.07	57.53+	—	—	—	35.15+	0.92
FJZP004	r tusk	70.15+	20.36							

Parameters after Tassy (2014). Plus marks (+) indicate minimal length due to the incomplete specimen.

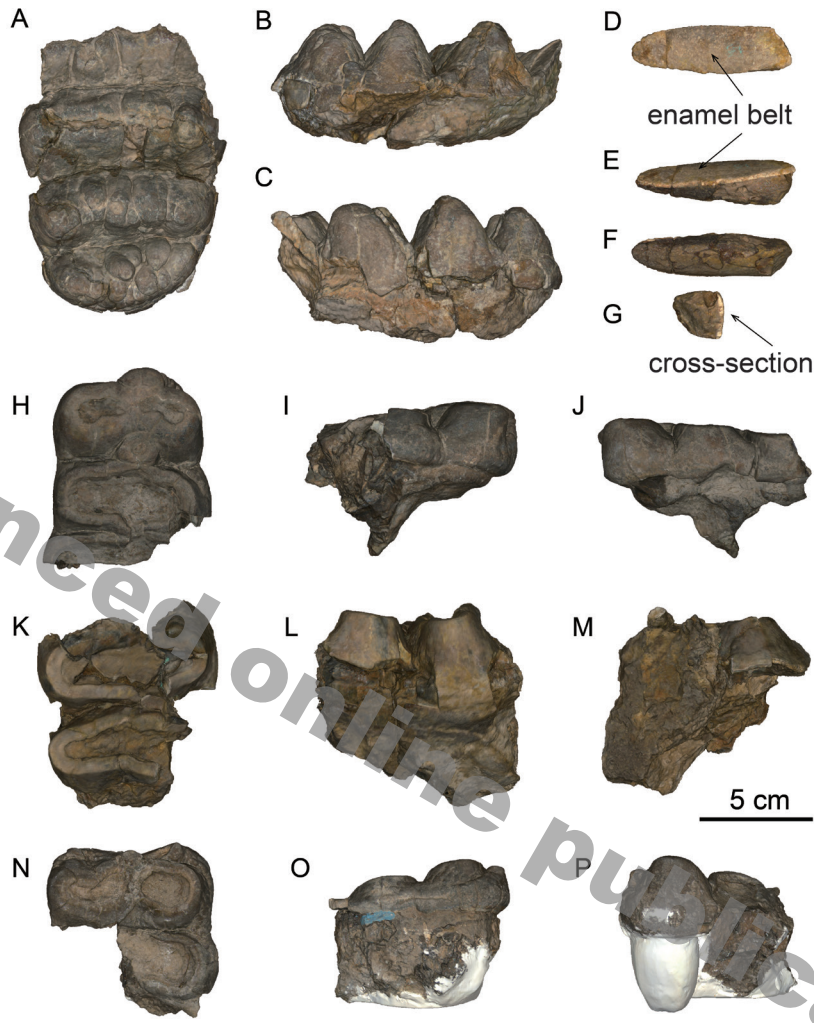

Fig. 4 Cheek teeth of *Stegolophodon pseudolatidens* from Zhangpu, Fujian Province, China
A–C. occlusal (A), lingual (B) and buccal (C) views of the left M3 (FJZP001);
D–G. Lateral (D), vertical (E) , ventral (F) views and the cross-section (G) of a right upper tusk tip (FJZP004);
H–J. occlusal (H), lingual (I) and buccal (J) views of the right lower m2 (FJZP002);
K–M. occlusal (K), lingual (L) and buccal (M) views of the M3 (FJZP003);
N–P. occlusal (N), lingual (O) and buccal (P) views of the left M2 (IVPP V33469)

5 Comparisons and discussion

5.1 Comparisons of the new material with the species of *Stegolophodon*

The new material exhibits the following morphological characteristics (Fig. 4). The tooth crown is notably low, and both the upper and lower molars are wider than those of gomphotheres, such as *Gomphotherium*, *Choerolophodon* and *Platybelodon*. The lophs/lophids

are very straight and oriented almost perpendicular to the long axis of the molar, and the interlophs/interlophids are relatively wide mesiodistally. The median sulcus is not prominent. The mesoconelets are well-developed, and there is a well-developed posterior cingulum, which tends to form an additional distal loph. The second posterior pretrite central conule is greatly reduced, which is representative of *Stegolophodon* morphology. Thus, the new material can be confidently attributed to *Stegolophodon*.

Tassy et al. (1992) reported *Sl. nasaiensis* from the Early Miocene locality of Na Sai, Thailand, making it the earliest known species of *Stegolophodon* (Fig. 5). *Sl. nasaiensis* is considered the most primitive *Stegolophodon*. The molar size is relatively small, and its m3 has five lophids. Compared to other species, the mesoconelet is weakly developed (Tassy et al., 1992). The molars of *Sl. pseudolatidens* are relatively small, with the M3 usually having 5 lophs, with the fifth lophs not completely developed. The posterior central conules of the main lophs on both the upper and lower molars are weakly developed or absent. The posterior lophs are nearly perpendicular to the long axis of the molar, and the two main lophs are almost aligned on the same horizontal plane (Yabe, 1950; Tomida et al., 2013).

Sl. hueiheensis, from the late Early Miocene of China, is closely similar to *Sl. pseudolatidens* from Japan, and the two have been informally grouped together as "*Stegolophodon* group 2" (Chow, 1959; Saegusa, 2008). Based on comparisons of mandibular morphology, Lizumi et al. (2021) illustrated that the mandibular morphology of *Sl. pseudolatidens* is as primitive as that of *Sl. hueiheensis*, *Sl. nasaiensis*, and *Sl. praelatidens*, and more primitive than *Sl.* cf. *Sl. stegodontoides*. However, the M3 and m3 of *Sl. hueiheensis* have only 4 lophs/lophids, and it is inferred that its M2 and m2 have only 3 lophs/lophids. Therefore, *Sl. hueiheensis* is more primitive and may not belong to *Stegolophodon*. Chow and Zhang (1983) classified *Sl. hueiheensis* into a new genus, *Rulengchia*, arguing that its intermediate cheek teeth are trilophodont rather than tetralophodont. We agree with this view, suggesting that *Stegolophodon* may have evolved from a group of trilophodont *Gomphotherium*-like taxa from East Asia during the Early Miocene, with"*Gomphotherium*" annectens as a potential candidate (Wang et al., 2023).

Koenigswald Von (1959) first reported a few fragmentary mastodont teeth from the lignite mine of Mae Moh, near Lampang (Fig. 5). This material was allocated to a new species, *Sl. praelatidens*, which was considered more primitive than the type species, *Sl. latidens*, from the Irrawady Formation of Burma. The M3 of *Sl. praelatidens* has 5 lophs, and the m3 has 6 lophids. The anterior and posterior central conules of the upper lophs are reduced, while the posterior central conules of the lower lophs are enlarged. The lophs are straight (Chavasseau et al., 2009). In contrast, the M3 of the type species, *Sl. latidens*, has 5.5 lophs with a well-developed posterior cingulum, which can be considered a half-loph. The mesoconelets of the first two main lophs are shifted forward and fused with the anterior central conules, while the

posterior central conules are relatively large. The first and second lophs form a "Y" shape and the remaining lophs are slightly chevroned (Saegusa, 2005; Li et al., 2020). *Stegolophodon cautleyi*, discovered on Perim Island, India, has relatively straight lophs. Its M3 has five lophs, and the interlophs are larger compared to other *Stegolophodon* species. In the first two lophs, the wear pattern on both sides of the pretrite half-loph and posttrite half-loph forms a "Y" shape (Osborn, 1936; Li et al., 2020; Lizumi et al., 2021). Another species, *Sl. stegodontoides* is more advanced. The M3 has six lophs with very weak anterior and posterior central conules, and the lophs are also relatively straight. The lower m3 has 7–8 lophids with weak anterior and posterior central conules. The lophids are slightly chevroned behind the third loph. Additionally, Zong (1992) and Saegusa et al. (2005) reattributed *Stegodon licenti* to *Stegolophodon* due to the presence of central conules on the second loph (lophid) of the molars. Interestingly, the median sulcus is very prominent in *Stegodon licenti*, and the second lophs of upper molars exhibit a somewhat "anancoid" morphology, which is rare among stegodontids. Therefore, *Stegodon licenti* possibly represents an unnamed genus of stegodontids.

The present material from the lower Fotan Formation at the Zhangpu locality, Fujian Province, represents a relatively primitive type of *Stegolophodon*, with the M3 exhibiting 5 lophs, the fifth loph being incompletely developed. The lophs/lophids are very straight

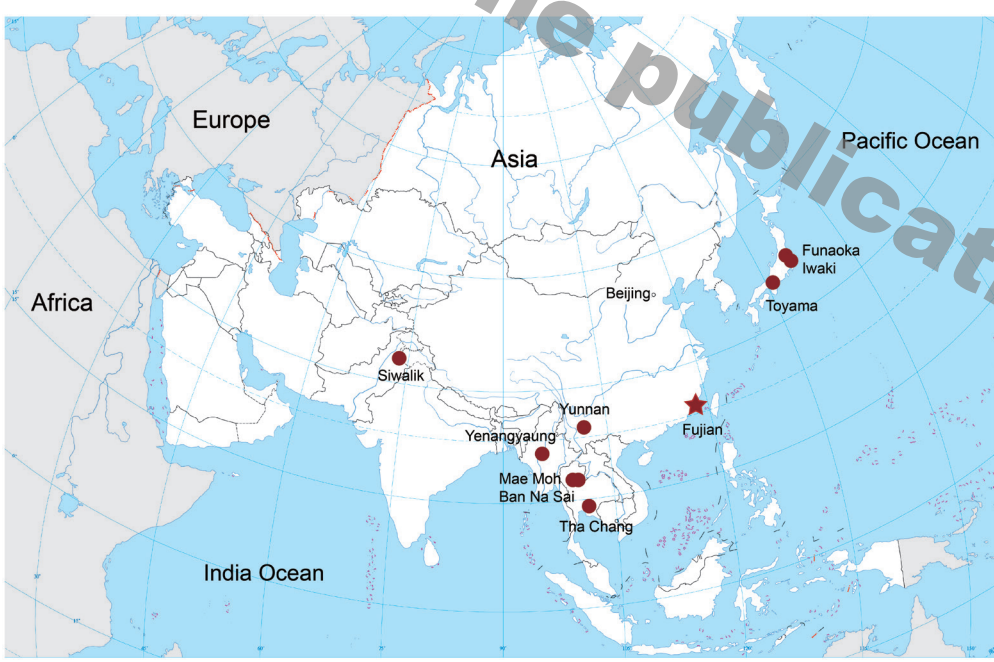

Fig. 5 Geographical distribution of *Stegolophodon* in Eurasia during the Miocene
The red star and red dots indicate the localities of *Stegolophodon*
Map Review (Inspection) Number: GS(2023)2752

and the mesoconelets are well-developed. These features are close to the *Sl. pseudolatidens*. Additionally, the second posterior pretrite central conule of both the upper and lower molars is much reduced. Therefore, there is no doubt that these new fossil materials can be attributed to *Sl. pseudolatidens*. In Japan, *Sl. pseudolatidens* is divided into three evolutionary stages, with its size decreasing from relatively large (stage 1, ~18–17 Ma) to medium (stage 2, ~17–16.5 Ma) to small (stage 3, ~16.5–16 Ma) (Saegus, 2008). The *Stegolophodon pseudolatidens* from Zhangpu, China, exhibits a large size similar to that of the Japanese *Sl. pseudolatidens* stage 1, despite the relatively later age of the Zhangpu specimens (~15.5 Ma).

The similarity between *Sl. pseudolatidens* from China and Japan suggests that there was faunal exchange and dispersal between the Early Miocene fauna of Japan and mainland China. Saegus (2008) proposed that there was a land connection between the Japanese islands and the Asian continent during the Early Miocene. Subsequently, sea levels gradually rose and remained high until the early Late Miocene, causing most of the original Japanese archipelago to become submerged (Hoshi et al., 2006). The reduction in island size led to the extreme dwarfism in *Stegolophodon* species on the Japanese islands (Saegus, 2008), whereas *Stegolophodon* in China retained a relatively large body size (Li et al., 2020).

5.2 The paleoenvironment of new *Stegolophodon pseudolatidens* materials

The Zhangpu biota from the Middle Miocene exhibits rich biodiversity, including biological material preserved in amber. Wang et al. (2021) suggested that the ecosystem in the Zhangpu area at that time was highly complex and diverse, potentially representing a tropical rainforest biome. The most diverse and fossil-rich plant groups within the Zhangpu flora include Dipterocarpaceae, Fabaceae, Lauraceae, and Clusiaceae, with Dipterocarpaceae being particularly notable as a dominant group in the present-day tropical rainforests of Southeast Asia. The vegetation of the Zhangpu area is classified as a tropical evergreen broadleaf forest, closely resembling the vegetation found in Central Thailand, Central India, and the Ganges Delta today (Shi et al., 2014). Research by Jacques et al. (2015) on ancient plants, along with the study of fossil fruits and seeds of the Lauraceae by Wang et al. (2019), revealed the vegetation composition and climatic conditions of that time. Their findings also confirmed that the Zhangpu area likely had a warm and humid climate conducive to the growth of tropical rainforests.

6 Conclusions

Based on the comparative analysis of molar morphology, the new materials from the Middle Miocene Fotan Formation in Zhangpu, Fujian Province, represent a relatively primitive form of *Stegolophodon*, which can be classified as *Stegolophodon pseudolatidens*.

The molars of *Stegolophodon* exhibit several common characteristics and evolutionary trends: tetralophodont, the M2/m2 have four lophs/lophids, the number of lophs/lophids on the M3/m3 gradually increases with the lophs/lophids becoming progressively straighter, the crown is relatively low, the the lophs/lophids are wider compared to those of Middle Miocene gomphotheres, the mesoconelets are well-developed, the anterior pretrite central conule is either fused with mesoconelets or completely absent, and the posterior central conules generally tend to degenerate.

This discovery marks the first fossil record of Neogene proboscideans in southeastern China, filling a significant gap in our understanding of the early evolution and distribution of *Stegolophodon* in this region. Furthermore, the presence of this species indicates a connection between the Middle Miocene mammalian faunas of Japan and East Asia, suggesting that faunal exchanges and dispersal occurred during the Early Miocene. The paleoenvironmental evidence further supports the idea that *Stegolophodon* was well-adapted to tropical forest environments, with its lineage persisting in East and Southeast Asia until the Late Pleistocene. This study provides crucial insights into the evolutionary history and biogeographical patterns of *Stegolophodon*.

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中国东南地区首次发现新近纪象化石

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摘要：脊棱齿象是一类在新近纪时期分布广泛，具有年代指示性的哺乳动物。近来在中国福建省漳浦地区中中新世佛昙组下部发现了脊棱齿象新化石材料，这是首次在中国东南地区发现新近纪的长鼻目化石。臼齿新材料齿冠较低，齿脊非常直，中沟不明显，中附锥和后齿带比较发达，第二后中心小尖明显退化；在形态上与*Stegolophodon pseudolatidens* (伪宽齿脊棱齿象)相似，可归属于同一物种。该发现不仅填补了新近纪时期该地区大型哺乳动物化石记录的空白，还为理解长鼻类的演化及古环境研究提供了宝贵信息。

关键词：中国东南，中中新世，长鼻目，脊棱齿象，形态学

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